



Biogeography of Beringian fishes after the molecular revolution and into the post-genomics era

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Abstract Significant progress in our knowledge of Beringian biodiversity and in the technologies available for biodiversity research has been made in the several decades since a comprehensive biogeographic synthesis of Beringian freshwater fishes was compiled and published in 1986. Further, the fish fauna of Beringia and, more broadly, of high latitude freshwater systems of the northern hemisphere face some

of the most intense well documented effects of global climate change. Here we synthesize current understanding of how the dynamic spatial and ecological landscapes of Pleistocene glaciations have shaped the distribution of taxonomic and genetic diversity in fish faunas of Beringia. Through a more complete integration of knowledge obtained in studies of fishes in Russian drainages, we aimed to identify promising strategies to test alternative biogeographic hypotheses on the roles played by the Bering land bridge, paleorivers and glacial history in intercontinental faunal movement. We focus on freshwater fishes of the Bering Strait region, which live in an environment that is premised on extreme instability and profound changes in long-term connectivity for fishes and offers opportunities to assess long-term evolutionary trends in both speciation and life history variation. Such information is critical for both our scientific understanding of evolutionary processes in fishes and valuable for those tasked with the challenges of management and conservation of natural resources in this expansive, dynamic and remote region. We provide an overview of Beringian freshwater ichthyofauna and examine genetic differentiation among population units within these lineages. We also examine evidence for how long population units have been separated based on historic glacially-related separations and the more recent marine barrier of the Bering Strait that constrains freshwater or diadromous species based on their ability to disperse in salt water. Our review concludes on how Arctic and sub-Arctic fishes may adapt

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and persist in their dynamic environment considering low genetic diversity, the role of adaptive introgression, and epigenetic variation. We find that Beringian fishes may poorly fit traditional taxonomic categories and the designation of conservation units below the species level may be of great practical application. Furthermore, as hybridization is documented to increase in the Arctic, the use of this process for ecological monitoring may also be of high utility with Beringian fishes.

Keywords Arctic · Beringia · Fishes · Phylogenetics · Phylogeography

Introduction

High latitude freshwater systems of the northern hemisphere have undergone, are undergoing, and are projected to undergo immense climatic changes. Paleoclimatic instability of the Pleistocene has been followed by rapid recent changes in the Arctic during the twentieth century (Moritz et al. 2002), with acidification of the Arctic Ocean for example, occurring at three to four times the rate of other ocean basins as result of melt-driven freshwater input in the twenty-first century (Qi et al. 2022). Despite these major ecological changes and the revolutionary developments in the ability to collect DNA sequence data, a comprehensive biogeographic synthesis of Beringian freshwater fishes has not been undertaken since Lindsey and McPhail (1986).

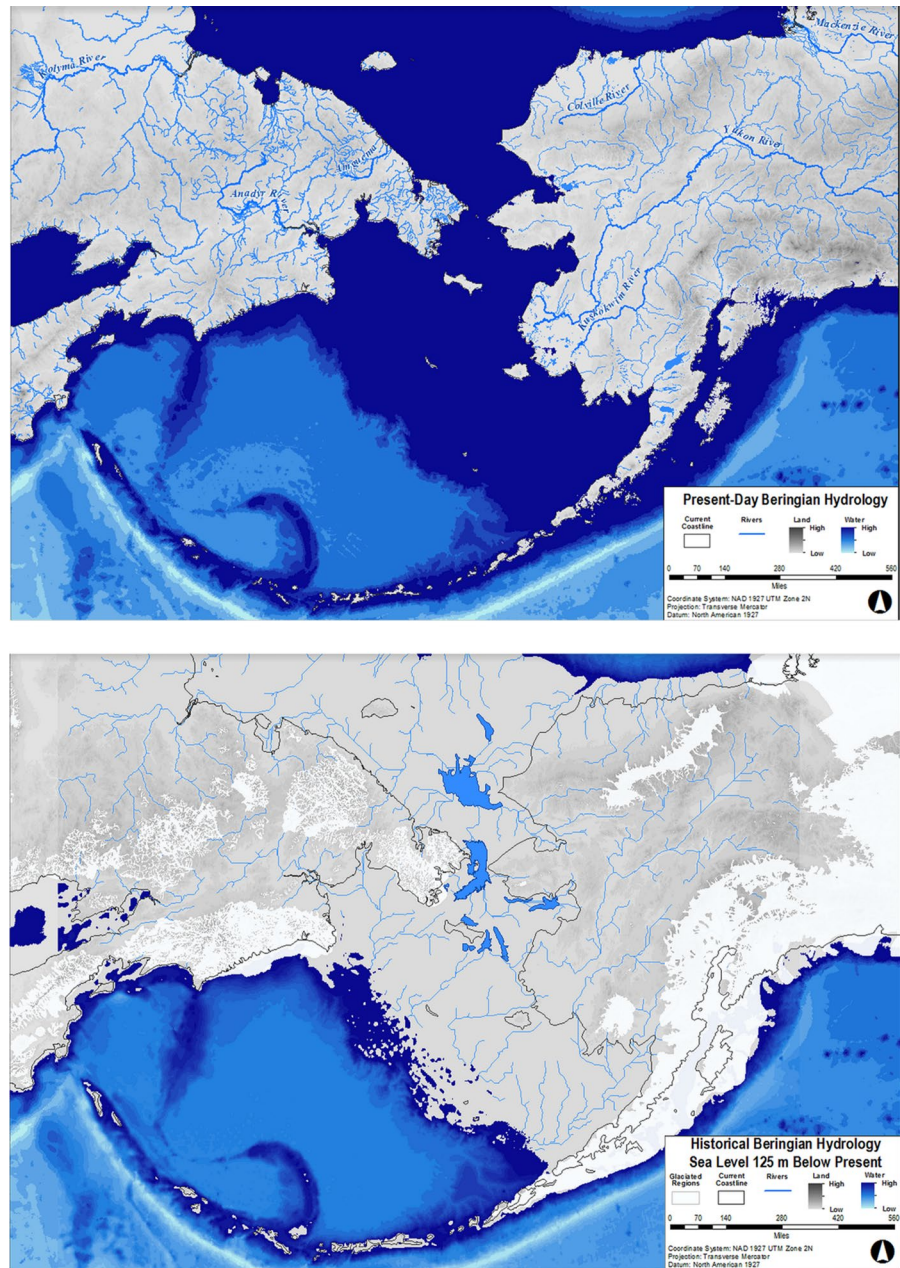
Beringia is a recognized biogeographic region encompassing the parts of northeastern Asia and northwestern North America surrounding the Bering Sea. Today the Bering Sea divides these two continents; however, during periods of lower sea-level stages the Bering land bridge allowed intercontinental exchange of diverse organisms (Pielou 1991; Fig. 1). Human migrations into Beringia and subsequent movement into the Americas constitute perhaps the most salient example of Bering land bridge mediated range expansion (Hoffecker et al. 1993). The term Beringia was coined out of recognition of the shared plant community (Hultén 1937), but is reflected in the freshwater fish community of the region as well. Modern freshwater fish assemblages in eastern Asia and northwestern North America have been divided by the sea for about 11,000 years (Elias et al. 1996), a

division intermittently breached by the emergence of the Bering land bridge resulting from paleoclimatic fluctuations of the Pleistocene (Lindsey and McPhail 1986). River drainage connections, coastal plains and coastal brackish waters over the Bering land bridge served as paths for dispersal for fishes unable to undertake marine migrations.

Freshwater habitats are restricted on the landscape, and during periods of Pleistocene glacial advance, suitable conditions for habitable freshwater systems became more limited. Freshwater fishes were then confined to refugia outside ice sheet-covered areas where conditions (e.g., extent of seasonal flows and freezing) remained suitable and connectivity facilitated range shifts in response to the evolving climate. Subsequently, in times of increased habitat availability and connectivity, post-glacial dispersal within and out of Beringia occurred (Hewitt 2000, 2004). Refugia themselves are of particular scientific interest as freshwater fishes would be expected to be subject to conditions favorable to speciation and rapid evolution (e.g. Campbell et al. 2015). During glacial maxima, freshwater fishes were subjected to strong selective pressures by environmental extremes, and genetic isolation among smaller populations. Post-glacially, these formerly isolated populations may reconnect or remain spatially or genetically isolated. Our knowledge of glacial refugia and dispersal is an essential component of understanding the processes generating and maintaining biodiversity within Beringia.

The freshwater fishes currently found in drainages surrounding the Bering Sea may be broadly divided into two classes based on salinity tolerance that relates directly to observed phylogeographic patterns (Table 1). These are primary freshwater fishes, which are almost exclusively in freshwater through their life cycle, and secondary freshwater fishes, which are generally restricted to freshwaters but may enter saltwater opportunistically or as part of life history strategies (Myers 1938). Primary and secondary freshwater fish species are expected to have distinct dispersal potential. Secondary freshwater fish species have much more mobility, including the ability to access different hydrographic basins through movements in coastal waters. In terms of surviving glaciations and recolonization of deglaciated habitats, there is a substantial advantage if coastal habitats may be utilized temporarily or for longer periods of time. The distances between some freshwater habitats exceed

Fig. 1 Present day hydrology of Beringia region and with sea level at 125 m below current levels as occurred during the Last Glacial Maximum



the distance solely across the Bering strait; however, the marine waters of Beringia are influenced by freshwater runoff. Therefore, they can provide opportunities for nearshore migration and dispersal of fishes with varying degrees of salinity tolerance. In the Arctic, the aggregate terrestrial runoff contributes to what is known as the Riverine Coastal Domain (Carmack et al. 2015) and the Bering Strait region receives substantial freshwater inputs via the warm, fresh Alaskan

Coastal Current in the eastern Bering Sea (Woodgate and Aagaard 2005), and the Siberian Coastal Current, running east along the coast of Chukotka (Weingartner et al. 1999).

Dispersal ability seems to be a key feature of Beringian freshwater fishes, as they are often widely-distributed (Lindsey and McPhail 1986). At one end of the spectrum, Burbot (*Lota lota*) and Northern Pike (*Esox lucius*) are primary freshwater fishes with

Table 1 Species or closely related species discussed together in this review. Taxa are divided into 1.0 Primary Freshwater Fishes, 2.0 Secondary Freshwater Fishes and 3.0 Amphidromous and Anadromous Fishes as in the text. Primary phylogeographic references are indicated along with the taxon's dispersal ability, saltwater tolerance and perceived ability to cross the Bering Strait under current conditions. A short summary of findings is also provided

Taxon	Primary phylogeographic Reference(s)	Dispersal ability	Saltwater tolerance	Likely to exchange across Bering Strait saltwaters?	Summary
1.0 Primary Freshwater Fishes					
Blackfishes					
<i>Dallia</i> spp.	Campbell et al. (2014); Campbell et al. (2015)	Low	Low	No	Shared genetic diversity between West Beringia and East Beringia, likely as a result of a shared Bering land bridge population being divided by rising sea levels. Multiple refugia present in East Beringia
Northern Pike	Skog et al. (2014)	Medium	Medium	No	Mitochondrial haplotypes shared across large distances. Evidence for multiple refugia during the last glacial maximum with expansion post-last glacial maximum
Burbot	van Houdt et al. (2005)	Medium	?	No	Beringian and Alaskan clades identified. Hypothesize that the Beringian clade dispersed from Siberia into Alaska via the Yukon Basin
Arctic Grayling	Stamford and Taylor (2004)	Medium	Low	No	North and South Beringian lineages reported, but considered conspecific across North America
Eurasian Graylings	Froufe et al. (2005)	Medium	Low	No	Unlike North America, Eurasia contains several potential species, but comprehensive geographic sampling is necessary to resolve outstanding questions
Pygmy Whitefish	Witt et al. (2011)	Low	Low	No	Presence of a Beringian clade, but West Beringia not evaluated

Table 1 (continued)

	Taxon	Primary phylogeographic Reference(s)	Dispersal ability	Saltwater tolerance	Likely to exchange across Bering Strait saltwaters?	Summary
Longnose Sucker	<i>Catostomus catus-tomus</i>	Bachevskaja et al. (2014); Dillinger et al. (1991)	Medium	Low	No	Evidence of Beringian clade present, low differentiation of Eurasian mtDNA haplotypes from North American
Slimy Sculpin	<i>Cottus cognatus</i>		Medium	High	No	No molecular phylogenetic or molecular phylogeographic study in Beringia
Lake Trout	<i>Salvelinus namaycush</i>		High	Medium	No	Lack of suitable habitat to facilitate colonization across the Bering land bridge may restrict species to East Beringia
Trout-Perch	<i>Percopsis omiscomaycus</i>		Med	Low	No	Lack of molecular data for relating Beringian fish to other North American <i>Percopsis</i> . Presumably entered the Yukon River from the Mackenzie River, but only found in East Beringia
Lake Chub	<i>Couesius plumbeus</i>	Taylor et al. (2013)	Med	Low	No	Presumably entered the Yukon River from the Mackenzie River, only found in East Beringia
2.0 Secondary Freshwater Fishes						
Round Whitefish	<i>Prosopium cylindraceum</i>	Morgan (2016); Morgan et al. (2018)	Medium	Medium	No	Clear signal of two Pleistocene refugia in North America, Eurasian sampling of three individuals contained distinct mitochondrial sequences from North America

Table 1 (continued)

Taxon	Primary phylogeographic Reference(s)	Dispersal ability	Saltwater tolerance	Likely to exchange across Bering Strait saltwaters?	Summary
Inconnu	<i>Stenodus leucichthys</i>	High	Medium	No	Likely to disperse along nearshore, reduced salinity environments. Genetic relationships and connectivity across the Bering Strait have not been evaluated
Broad Whitefish	<i>Coregonus nasus</i>	Medium	?	No	Eurasian Broad Whitefish poorly characterized genetically, morphological similarity across Bering Strait would indicate Anadyr River fish are more similar to Alaskan fish (Reshetnikov 1975)
Arctic Cisco	<i>Coregonus autumn-nalis</i>	High	High	Yes	Very little genetic differentiation is apparent between Eurasian and North American Arctic Cisco, unclear if this is a result of recent divergence, ongoing migration or a combination of these factors
Bering Cisco	<i>Coregonus laureitae</i>	High	High	Yes	Predominately East Beringian, has been observed in Northwestern Beringia, but only known spawning locations are in East Beringia. Origins of West Beringian fish need to be ascertained

Table 1 (continued)

Taxon	Primary phylogeographic Reference(s)	Dispersal ability	Saltwater tolerance	Likely to exchange across Bering Strait saltwaters?	Summary
Lake Whitefish Complex <i>Coregonus</i> spp.		Medium	Medium	No	No comprehensive molecular phylogeographic study of this species complex across Beringia has been conducted. Two members may be of ancient hybrid origin, but these hypotheses, timing and location of hybridizations have not been evaluated
Least Cisco Complex <i>Coregonus</i> spp.	Padula et al. (2017)	Medium	Medium	No	Least Cisco Complex represented by one species in Beringia, the Least Cisco <i>C. sardinella</i> with life history diversity, ecotypic diversity and population genetic structure poorly known across its range. Padula et al. (2017) examined East Beringian Least Cisco identifying three broad geographic groupings
3.0 Amphidromous and Anadromous Fishes Arctic Lamprey Complex <i>Lethenteron</i> spp.		High	High	Yes	A complex of both migratory and resident life history forms. Nominal species in Beringia may be life history variants of the same species, and taxonomic revision of these fishes is likely warranted
Pond Smelt <i>Hypomesus olidus</i>		High	High	Yes	Composed of vastly separated sub ranges within Beringia of unclear taxonomic certainty

Table 1 (continued)

Taxon	Primary phylogeographic Reference(s)	Dispersal ability	Saltwater tolerance	Likely to exchange across Bering Strait saltwaters?	Summary
Pacific Rainbow Smelt	Kovpak et al. (2011)	High	High	Yes	Some phylogeographic study of West Beringia, but no study with representative sampling of Beringia. Scientific documentation of possible ecotypes is likely incomplete
Arctic Charr Complex	Taylor (2016); Moore et al. (2015)	High	High	Yes	Taxonomic diversity not well understood and comprehensive sampling needed to resolve. Two lineages in Arctic Charr <i>S. alpinus</i> identified in Beringia, "Beringian" and "Arctic", survival of this charr in both North and South Beringia during the last glacial maximum
Threespine Stickleback	Ortí et al. (1994); Chythlook (2000)	Medium	High	Yes	Sampling has focused on coastal populations with anadromous components. Characterizing inland populations can provide insight into the species survival through the Pleistocene
Ninespine Stickleback	Aldenhoven et al. (2010)	Medium	High	Yes	Distinct lineages in North American may correspond to Beringian and Mississippian refugia. Survival in Beringia may originate from freshwater sub-refugia although the fish is capable of utilizing marine waters

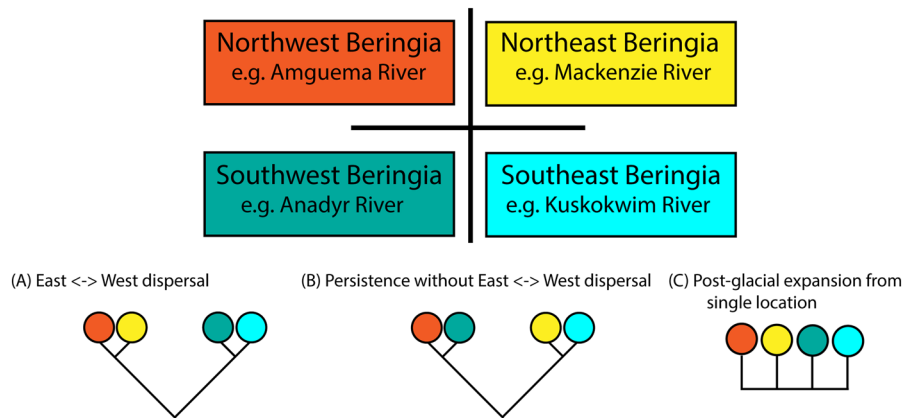


Fig. 2 Conceptual models of phylogenetic relationships of a species across Beringia. With four major provinces of Beringia, **A** dispersal across an East–West axis would result in North–South divide in a species; **B** Persistence on either side of the Bering strait without East–West dispersal would create

and East–West divide in a species; **C** Post-glacial expansion from a single location to a Beringia-wide distribution would generate poorly resolved relationships among the four major provinces

circumpolar distributions, and tolerance to low salinity conditions is only documented in populations of Northern Pike from the Baltic Sea (Rohtla et al. 2012, 2014). At the other end, endemism is low in Beringia, and exhibited by a single genus of primary freshwater fish, blackfishes, *Dallia* (Esociformes: Esocidae). *Dallia* is represented by 1–3 nominal species found only in Beringia (Balushkin and Chereshev 1982; Campbell et al. 2015; Campbell and Lopéz 2014; Chereshev and Balushkin 1981; Lindsey and McPhail 1986). Blackfishes are small, sedentary fish occasionally found in coastal lagoons with variable salinity. Body size, behavior and low salinity tolerance suggest the Bering Sea is an impassable barrier and thus no migration between Asian and North American populations is likely over the past 11,000 years. Among secondary freshwater fishes, broad distributions that span well outside Beringian drainages are most common (e.g., the holarctic Arctic Charr, *Salvelinus alpinus*). A notable exception to this pattern is the Beringia endemic Bering Cisco (*Coregonus laurettae*), which is only documented spawning in locations in the Yukon, Kuskokwim and Susitna Rivers in East Beringia, but has been reported in West Beringia (Chereshev 1984).

Species with similar habitat requirements may be expected to also share biogeographic histories. They may persist in the same refugia and disperse using similar routes leading to common geographic

distribution patterns among species and populations (e.g. Fig. 2). This phylogeographic concordance is well-documented in temperate latitudes, but declines in the north (Bernatchez and Wilson 1998). In Beringia, freshwater fishes generally exhibit low phylogeographic concordance and relatively low intraspecific genetic diversity (Bernatchez and Wilson 1998; Campbell and Lopéz 2014). Differential survival and dispersal of genotypes leads to different phylogeographic patterns among Beringian species; therefore, the histories of individual lineages are complex and unique. Here, we summarize the state of knowledge of Beringian freshwater fishes and identify knowledge gaps in understanding their histories. While phylogeographic concordance among Beringian fishes is low, these different histories can inform us on the strategies Beringian fishes used to adapt and persist in this dynamic and extreme landscapes.

In this review we focus on fishes that spawn in freshwater and have geographic ranges that include Beringia (Table 1). Our review focuses on taxonomic groups that have received relatively little attention in studies of biodiversity and evolutionary genetics. Pacific salmon (*Oncorhynchus* spp.) are not specifically discussed in this review as they are the subject of substantial research (e.g. Khrestaleva 2016; Tarpey et al. 2018); however, we draw in elements of that literature in our discussion. Additionally, diversity and distribution patterns of charrs (*Salvelinus* spp.) were

recently reviewed with a largely North American focus (Muir et al. 2021; Taylor 2016) therefore those species are not extensively treated here.

Here, we summarize existing knowledge of how the Pleistocene glaciations and associated dynamic spatial and ecological landscapes influenced taxonomic and genetic diversity in Beringian freshwater fish fauna. We attempt to unify the biogeographic region that is divided politically and intellectually with a more complete incorporation of knowledge obtained from West Beringian drainages. Throughout the review we identify shortfalls in understanding and directions for future scientific inquiry with Beringian freshwater fishes not only centered on biogeography, but also other evolutionary questions that can now be addressed with new technologies.

1.0 Primary Freshwater Fishes

Blackfishes *Dallia* spp. (Esociformes)

Dallia is an esociform genus comprising two species of Blackfish currently considered valid: *D. admirabilis* of the Amguema River basin and the more widespread Alaska Blackfish *D. pectoralis* (Fricke et al. 2023). Blackfishes are unique among extant fishes by virtue of being exclusively found in Beringian freshwaters. Molecular evidence on the phylogenetic relationships among esociform lineages indicates that early proposals placing *Dallia* among a monophyletic group of mudminnow genera are incorrect (López et al. 2004). Available evidence supports *Dallia* as the living esociform lineage most closely related to a group formed by pikes (*Esox*), pickerels (*Esox*), and the Olympic Mudminnow *Novumbra hubbsi* (Betancur-R et al. 2013; Campbell et al. 2013). All known populations of *Dallia* are restricted to freshwater habitats, although there are a few records of the Alaska Blackfish occupying brackish coastal lagoons where salinity averaged 2.42 ppt (Fraley et al. 2022). Blackfishes are small-bodied fish with adult lengths around 12 cm and a largely sedentary, benthic lifestyle capable of breathing air. Considering the external anatomy, behavior and physiology of blackfishes, it is reasonable to assume that the Bering Sea represents an unsurmountable barrier to their movement between continents and distant river basins. In contrast, extensive river deltas, seasonally flooded coastal

plains and wetlands are likely to form suitable routes for Blackfish to disperse across low relief landscapes. Increased knowledge of the timing, topology, hydrography, and environments of the Bering land bridge will be essential to understanding how the distribution and diversity of present blackfish species and populations was shaped by glaciation dynamics.

The effects of paleoclimatic variability on the distribution of genetic variation on extant populations of *Dallia* and their demographic history have been examined using evidence from mitochondrial and nuclear DNA sequences (Campbell et al. 2015; Campbell and Lopéz 2014). The evidence suggests four distinct historical Beringian refugia, broadly corresponding to: (1) the Arctic Coastal Plain of Alaska, (2) West-Central Alaska, (3) Interior Alaska, and (4) the Bering coasts grouping southwest Alaska, St. Lawrence Island, and Chukotka. The genetic cluster now found in the Bering coasts point to the Bering land bridge itself serving as a large regional refugium and route from where the Alaska Blackfish expanded westward into Chukotka. The available fossil evidence is very limited and subject of debate but it points to a broader historical distribution for *Dallia* spp. extending at least to the Kolyma River in the west and in North America including Pacific Ocean drainages on the Kenai Peninsula of Alaska (Cavender 1969; Gaudant 2012; Sytchevskaya 1968). If the fossil material is correctly assigned to *Dallia* then the history of the genus involves extirpation from major regions associated with Beringia.

The examination of this primary freshwater fish with no expected ability to cross the Bering Strait did, however, show levels of genetic similarity compatible with high levels of migration between East and West Beringia (Campbell et al. 2015). This finding is a result of past connectivity across the Bering land bridge as opposed to current exchange of individuals. A high degree of genetic structuring may be expected in *Dallia* as it is small, not a strong swimmer, is not known to undertake long-distance migrations, is presumably intolerant of salt water, and is capable of survival in marginal habitats through cold- and hypoxia-tolerance combined with air-breathing (though see Campbell et al. (2014) for a case of mass die-off) (Campbell 2011).

The studies of Campbell and Lopéz (2014) and Campbell et al. (2015) did not examine all the described species, with only one population (n=8

individuals) sequenced for mitochondrial data from *D. admirabilis*. The remainder of locations examined by Campbell and Lopéz (2014) and Campbell et al. (2015) are considered to be *D. pectoralis* (Balushkin and Chereshnev 1982). Thus, the species *D. delicatissima*, considered valid by Balushkin and Chereshnev (1982), was not examined in either study. Further refinement of the systematics of the genus can be accomplished with a thorough representation of sequence data from *D. admirabilis* and *D. delicatissima* placed in a geographically wide-ranging data set of *Dallia*, such as those generated by Campbell and Lopéz (2014) and Campbell et al. (2015).

Northern Pike *Esox lucius* (Esociformes)

Northern Pike *Esox lucius* have a very broad circumpolar distribution and are large ambush predators (Craig 1996). Often considered a freshwater fish, Northern Pike inhabit the brackish waters of the Baltic and Caspian Seas and may exhibit an anadromous life history (Skov and Nilsson 2018). Northern Pike have long been considered to have extremely little genetic diversity—particularly in North America (e.g., Senanan and Kapuscinski 2000). Examination of allozymes across North America revealed only two polymorphic loci out of 65 with an average observed heterozygosity of 0.001 (Seeb et al. 1987), a result that remains supported by additional studies with a variety of genetic techniques. The low genetic diversity observed among Northern Pike populations may be a product of small population sizes as a result of being a top predator (Healy and Mulcahy 1980). However, additional studies of Northern Pike have revealed increased genetic diversity in Southern Europe that has coincided with the description of two species—*E. aquitanicus* from Southwest France and *E. cisalpinus* from Italy (Bianco and Delmastro 2011; Denys et al. 2014; Lucentini et al. 2011). These species persisted south of major ice sheets in Western Europe during the Pleistocene, and Northern Pike also appear to have two European refugia (Skog et al. 2014). Beringian *Esox* mitochondrial haplotypes belong to a larger Holarctic clade of mitochondrial lineages with a wide distribution originating from East Asia (Skog et al. 2014). Examination of ancient DNA from an *E. lucius* specimen from Alaska supports a single expansion of *E. lucius* across North

America from Alaska within the last ~100,000 years (Wooller et al. 2015).

Phylogeographic studies of Northern Pike have largely been restricted geographically (Maes et al. 2003; Nicod et al. 2004; Skov and Nilsson 2018). The most comprehensive study to date only examined one population in East Beringia and one in West Beringia (Skog et al. 2014). Analysis of both East and West Beringian population samples of Northern Pike may be limited due to the possible absence of Northern Pike from the Chukchi Peninsula (Chereshnev 1979; Craig 1996). Nonetheless, this species appears to be widely distributed elsewhere in East and West Beringia. To what extent pike survived in sub-refugia within Beringia is unclear and how many migrations from Asia or North America into Beringia occurred with this species. Despite the capacity of the species to tolerate some salinity (e.g. Jalbert et al. 2021) current salinity levels in the Bering Strait most likely remain too high for this species to disperse across.

Burbot *Lota lota* (Gadiformes)

Burbot *Lota lota* are notable in being the only completely freshwater cod (Gadiformes), with evidence of freshwater occupancy by this genus in the Early Pliocene (Pietschmann 1934). Although fossil evidence would support that the genus has at least five million years of history in freshwaters, the various species described in *Lota* are best characterized by two subspecies *Lota lota lota* and *Lota lota maculosa* (Van Houdt et al. 2003). The Holarctic distribution of *L. lota* is composed of *L. l. lota* from Western Europe through Beringia into the Yukon River basin. The remainder of the North American range of this species is composed of *L. l. maculosa* with some admixture between subspecies detected at Great Slave Lake and Lake Laberge (Elmer et al. 2008).

Beringia has been crucial in the expansion and survival of this species with non-molecular evidence pointing to a Palearctic origin of this species and molecular evidence pointing towards a Nearctic origin. The implications are that the Burbot originated in the Palearctic, dispersed into the Nearctic and North America, and then was reduced to a single (i.e. Beringian) ancestral *L. l. lota* population (Houdt et al. 2005). Evidence of a Palearctic origin of Burbot comes from the distributions of its near relatives and the fossil record. The nearest relatives of Burbot

are four species classified in the genera *Brosme* and *Molva* and all together comprise the gadid subfamily Lotinae (Nelson 1994). All members of the Lotinae except Burbot are found in the East Atlantic Ocean (Cohen et al. 1990). Fossil evidence for *Lota* in North America is from 60,000–10,000 years ago (Cumbaa et al. 1981) contrasted against the five million year old evidence in Central Europe (Pietschmann 1934). The age of *Lota* dates to the Late Miocene (Van Houdt et al. 2003) while the *L. l. lota* mitochondrial lineage is on average ~1.25 to ~2.0%, depending on the locus, from that of *L. l. maculosa* supporting a Pleistocene separation and diversification of the two lineages (Houdt et al. 2005). Mitochondrial gene sequencing of *L. l. lota* reveals two widespread ancestral haplotypes from Central Europe to East Beringia representing most fish with 28 additional haplotypes and indicates *L. l. lota* expanded across its range 240,000–130,000 years ago (Houdt et al. 2005). Variation within North America indicates that *L. l. maculosa* lineages began diverging within the last 700,000 years, therefore exhibiting a greater intra-subspecific coalescence time.

Investigations of Burbot have indicated the role of the Beringian refugium in facilitating intercontinental exchange, yet resolution within Beringia for sampling has been low for this species. Therefore the subdivision present within Beringian mitochondrial lineages (Houdt et al. 2005) cannot currently be placed to originating on an East–West or North–South axis within Beringia.

Grayling *Thymallus* spp. (Salmoniformes)

The Arctic Grayling *Thymallus arcticus* inhabits clear and cold rivers, streams and lakes with high oxygen content (Kottelat and Freyhof 2007). While potentially able to transit coastal and marine environments, Arctic Grayling only rarely have been captured in nearshore waters (e.g. Fechtel et al. 2006) nor do they exhibit high salinity tolerance (100% mortality in 50% seawater within 100 h) (Blair et al. 2016; Northcote 1995). Therefore, the current distribution of Arctic Grayling is overwhelmingly shaped by freshwater connectivity. Arctic Grayling overlap in distribution with the European Grayling *T. thymallus* at the Kara River in Siberia (Janković, 1964), but the range of Arctic Grayling in Eurasia is largely restricted to coastal

areas in West Beringia (including St. Lawrence Island, based on proximity to the Eurasian coast-line). Arctic Grayling is distributed farther inland and in coastal areas elsewhere in Eurasia occurring in the Ob, Yenisey, and Lena rivers (Weiss et al. 2007). In North America, Arctic Grayling are distributed throughout the north-west of the continent (Alaska, Yukon, Northwest Territories, northern British Columbia, Alberta, Saskatchewan and Manitoba) (Northcote 1995). An isolated native population is present in Montana (Kovach et al. 2020) and another glacial relict Michigan population has become extinct (Vincent 1962).

Throughout its North American range, Arctic Grayling is considered to be a single taxon while in Eurasia several subspecies or closely related species may be recognized (Redenbach and Taylor 2002; Stamford and Taylor 2004; Weiss et al. 2006, 2007). Mitochondrial phylogeographic studies do support separate refugia within North America, with clear signals from North Beringia (North of Brooks Range mountains), South Beringia (South of Brooks Range) and the Nahanni River region without indications of long term persistence in refugia leading to speciation (Stamford and Taylor 2004). In contrast, graylings have diversified in West Beringia with several taxa having been recognized based on morphological and life history differences, e.g. *T. arcticus mertensi* and *T. arcticus signifler* (Skopets 1991; Skopets and Prokop'yev 1990) with mitochondrial data supporting the concept of several species in eastern Eurasia closely related to *T. arcticus* (Froufe et al. 2005).

Clear resolution of Grayling systematics in West Beringia is contingent on sampling several locations within large drainage basins and more completely representing populations from a taxon (Froufe et al. 2005). Increasing geographic and population sampling has continued to reveal new distinct lineages of *Thymallus* that may be sympatric (Antonov 2004; Knizhin et al. 2004, 2007; Knizhin and Weiss 2009; Weiss et al. 2006, 2007).

Pygmy Whitefish *Prosopium coulteri* (Salmoniformes)

Pygmy Whitefish *Prosopium coulteri* have been documented in numerous lakes and a few streams in drainage systems across North America from

Atlantic coast drainages including the Saint Lawrence and Nelson rivers (Eschmeyer and Bailey 1955; Lindsey and Franzin 1972), the Mackenzie River draining into the Beaufort Sea (Lindsey and Franzin 1972; Vecsei and Panayi 2015), the upper Yukon River and several Pacific coast drainages from the Columbia River to the Alaska Peninsula (McCart 1970; Bird and Roberson 1979; Wiedmer et al. 2010). Pygmy Whitefish have also been found in numerous lakes within Bering Sea drainages in southwest Alaska (Heard and Hartman 1965; McCart 1970; Russell 1980; Plumb 2006). In West Beringia, Pygmy Whitefish have been documented from only four lakes in the Amguema River drainage in Eurasia (Chereshnev and Skopets 1992). The distribution of Pygmy Whitefish is still being characterized and is expected to be further refined. It is probable that during the late Pleistocene the Pygmy Whitefish was more continuously distributed along the margins of ice sheets, with the current distribution explained by survival in suitable habitat and the end of the Wisconsinan glacial period (Eschmeyer and Bailey 1955; Lindsey and McPhail 1986; Wiedmer, et al. 2010).

In their survey of widespread anatomical differentiation in Pygmy Whitefish, Eschmeyer and Bailey (1955) stated that their observations were more consistent with ecological differences rather than fundamental divergences. Genetic study of Pygmy Whitefish in North America did indicate two distinctive clades (1) Southwest Alaska and the Alek River, and (2) Cascadia, Mackenzie River, and Lake Superior. Average divergence between these two clades may be equivalent to 1.65–3.3 million years (Witt et al. 2011). North American Pygmy Whitefish may have originated from two locations given the results of Witt et al. (2011), Beringia and Cascadia. Explanation of how fish may have reached Lake Superior from Cascadia is complex, and Witt et al. (2011) suggest post-glacial dispersal at the end of the Wisconsinan glaciation from three refugia—Beringia, Cascadia, and the Mississippi refugium—a suggestion similarly supported by Blanchfield et al. (2014).

Investigation at finer spatial scales with microsatellite data has demonstrated little genetic differentiation that may be promoted by spawning at a relative young age, moving into rivers to spawn leading to genetic connections between different lakes, and large

population sizes (Taylor et al. 2011). The genetic differentiation observed also could be largely explained by geographic distance between sampling locations. However, Pygmy Whitefish exhibit morphological divergences within lakes, indicating ecological speciation with evidence of genetic differentiation between ecotypes, e.g. Gowell et al. (2012).

The genealogical relationships of Pygmy Whitefish in West Beringia have not been assessed, and the degree of differentiation from North American populations is unknown. With the biology of this species, some differentiation may be expected across the Bering Strait. When did West Beringia Pygmy Whitefish separate from those in North America? Given the history of increasing occurrence data in North America, is the Amguema River basin the only location of Pygmy Whitefish populations in West Beringia? The Amguema River basin has been recognized as a Beringian sub-refugium (e.g. Balushkin and Chereshnev 1982; Chereshnev and Balushkin 1981), and timing of Pygmy Whitefish divergences will inform this hypothesis. In addition to examining trans-Beringian relationships from a genetic perspective within this species, incorporating morphological measurements to identify ecological species within Eurasian populations should be undertaken.

Longnose Sucker *Catostomus catostomus* (Cypriniformes)

The Longnose Sucker *Catostomus catostomus* is a freshwater fish that has a large North American range, but does not have an extensive Asian distribution (Lindsey and McPhail 1986). While present from the Great Lakes northward largely throughout Canada and Alaska (Scott and Crossman 1973), this species occupies a limited range in Asia being absent from the Chukotka Peninsula, Amguema River, and, the Anadyr River (Andreev and Reshetnikov 1981). In Asia, the Longnose Sucker is known from the Kolyma River and mitochondrial cytochrome oxidase I (COI) sequences from that location show little differentiation from those in North America (Bachevskaja et al. 2014), despite purported intolerance of saltwater. Current sampling from both Asia and North America are much too scant to provide a range-wide phylogeographic perspective on this species; however, given the geographic isolation of the Siberian Sucker (*C. catostomus rostratus*)—across the Bering

Strait and the Chukotka Peninsula—it represents an independent evolutionary unit of this species.

The Longnose Sucker belongs to an entirely polyploid family that originated approximately 50 million years ago in which the common ancestor underwent a whole-genome duplication (WGD) (Uyeno and Smith 1972). Polyploid fishes are known from several families, most notably the Salmonidae which receives the bulk of study on this phenomenon in fishes (Allendorf and Thorgaard 1984; Berthelot et al. 2014; Lien et al. 2016). Thus, catostomids represent an opportunity to study the effects of WGD within fishes as an alternative to salmonids and co-occur geographically (e.g. Krabbenhoft et al. 2021).

Slimy Sculpin *Cottus cognatus* (Scorpaeniformes)

The Slimy Sculpin (*Cottus cognatus*) is widely distributed in North America but occupies a restricted distribution in Eurasia. The Slimy Sculpin is found on the Chukotka Peninsula, the Anadyr River and the Amguema River. Lindsey and McPhail (1986) hypothesize this species crossed the Bering land bridge and was able to enter paleorivers, both the Chukchi Sea River and the Anadyr Gulf River, leading to its current distribution during the Wisconsin glacial period. This hypothesis is supported by the distribution of morphological variation in this species. Morphological variation across the range is extensive, and concordant with persistence and dispersal from multiple refugia (McAllister and Lindsey 1961). This morphological variation indicates that West Beringian Slimy Sculpin have not diverged from East Beringian Slimy Sculpin due to a high degree of similarity (Chereshnev 1976), despite the unlikelihood of ongoing migration across the Bering Sea because of the fish's small body size, presumed intolerance of saline waters, and small home range (Gray et al. 2004). There has been no molecular phylogenetic perspective on the phylogeography of this species within Beringia. A molecular perspective and widespread sampling would test the morphologically-based hypothesis of relationships, identify any cryptic species (e.g. Moyle and Campbell 2022), identify if there is a North–South Beringian divide in this species and provide some guidelines for dating the divergence of East and West Beringian Slimy Sculpin.

Primary freshwater fishes found only in East or West Beringia

Several species of fish of a diverse taxonomic background are found only in East or West Beringia. In East Beringia, the salmoniform Lake Trout (*Salvelinus namaycush*), percopsiform Trout-Perch (*Percopsis omiscomaycus*) and the cypriniform Lake Chub (*Couesius plumbeus*) are not found in West Beringia although they are widely-distributed elsewhere. Conversely, the cypriniform Eurasian Minnow (*Phoxinus phoxinus*) approaches the Bering Strait but doesn't cross into East Beringia. The salmonid Lake Trout has near relatives that are widely distributed, but the other species are the only representatives of their taxonomic orders in Beringia (Cypriniformes, Percopsiformes).

Why have these species not crossed intercontinentally? Considering Lake Trout, evidence indicates that it is a long-term inhabitant of Beringia that has not successfully dispersed further westwards with a distribution that largely mirrors the extent of glaciers during the Pleistocene. This species has been documented to colonize lakes via rivers (Muhfeld et al. 2012) and in four populations anadromy of limited (<50 km) distance has been observed (Harris et al. 2014). Both cases indicate strong dispersal potential across waterscapes. Indeed, post-glacial expansion in North America from Beringia outwards and from the Nahanni refugium into Beringia have been hypothesized based on a phylogeographic study (Wilson and Hebert 1998). It is possible that lack of suitable habitat to facilitate colonization west across the Bering land bridge was the main limiter of dispersion. Lake Trout are typically found in deep, clear and rocky-bottomed lakes generated by glacial scour in which they also spawn (Martin and Olver 1980), and these habitats were likely sparse along the Bering land bridge.

Trout-Perch and Lake Chub, however, occupy the Yukon and Mackenzie Rivers yet do not occur in West Beringia. They are small-bodied and poor swimmers compared to Lake Trout and are not known to disperse through coastal or marine waters (Taylor et al. 2013; Warren and Burr 2014), perhaps explaining their inability to cross the Bering Strait. The Eurasian Minnow is found in West Beringia across the Chukotka Peninsula and in the Amguema River and is similarly limited in dispersal ability (Lindsey and McPhail 1986), being absent from East Beringia.

It is worth noting that species of *Chrosomus* found in North America outside Beringia were considered closely related *Phoxinus* and at times classified in the same genus (e.g., Banareescu 1964; Howes 1985). Lindsey and McPhail (1986) interpreted this as evidence *Phoxinus* crossed the Bering Strait prior to the Pleistocene. Current thought, based on molecular phylogenetics, is that *Phoxinus* has been restricted to Eurasia and *Chrosomus* has been found to be most closely related to other North American cyprinids (Schoenhuth et al. 2012; Strange and Mayden 2009). In light of these findings, it does not appear that *Phoxinus* crossed the Bering Strait and established populations in East Beringia or elsewhere in North America, at least none that persisted.

2.0 Secondary Freshwater Fishes

Coregoninae (Salmoniformes)

Coregonines have a circumpolar distribution with hot-spots of described species diversity in eastern North America and northwestern Eurasia (Nelson et al. 2016). They are a substantial component of Beringian freshwater fish diversity exhibiting diverse morphologies, life histories and ecologies. A complete understanding of the taxonomy, and species-level diversity of Coregoninae is challenged by numerous factors such as post-Last Glacial Maximum (LGM) adaptive radiation, hybridization, ecological speciation, a paucity of distinguishing anatomical features, morphological convergence and a lack of standardization among genetic studies (e.g. Douglas et al. 1999; Præbel et al. 2013). The number of species of Coregoninae is up for debate, with 91–92 species listed in Eschmeyer’s Catalog of Fishes and FishBase in recent years (Fricke et al. 2021, 2023; Froese and Pauly 2019). Fishes of the World 4th edition lists 32, and “as many as 88” in the 5th edition (Nelson 2006; Nelson et al. 2016). As such, a precise species number of coregonines across the range is hard to ascertain and generating a species checklist for Beringia certainly is problematic. Overall, fewer species are recognized in Beringia in comparison to Western Europe or Eastern North America, a potential result of less scientific effort in Beringia compared to other regions or perhaps a consequence of biological processes generating more species through adaptive radiations into

large lake habitats or speciation occurring around the periphery of continental ice sheets.

The number of genera in Coregoninae is widely accepted to be three—*Prosopium*, *Stenodus*, and *Coregonus*. To provide a reference to relationships within Coregoninae for the reader, we compiled existing mitochondrial COI data to create a phylogeny (Supplemental Figure S1). The monophyly of *Prosopium* is widely accepted, and to date constitutes few (6) of the recognized species in the genus. *Stenodus* comprises 1–2 species and is anatomically distinctive, yet, molecular phylogenetic studies do not always resolve this genus as distinct from *Coregonus* (e.g. Bernatchez et al. 1991; Bodaly et al. 1991; Campbell et al. 2020; Lockwood et al. 1993) and Supplemental Figure S1. Consequently, some authors contend that *Stenodus* species should be reclassified into *Coregonus* (e.g. Stott and Todd 2007). Species diversity of the genus *Coregonus* remains largely unresolved, does not integrate well with traditional taxonomy, and is challenging to define conservation units with.

Looking across taxonomic units, it is clearer to divide coregonines into several classes based on the clarity of phylogenetic resolution and geographic distribution for discussion here. Focusing on Beringia, there appear to be several species within well-defined taxonomic units distributed in both East and West Beringia composed of conspecific populations. These are Round Whitefish (*Prosopium cylindraceum*), Inconnu (*Stenodus leucichthys*), Broad Whitefish (*Coregonus nasus*) and Arctic Cisco (*Coregonus autumnalis*). There are also two predominantly North American species with Asian isolates—Pygmy Whitefish (*Prosopium coulteri*), which we discussed above, and Bering Cisco (*Coregonus laurettae*). Other coregonines are widely-distributed and best described as species complexes and discussed as such—Lake Whitefish Complex (*Coregonus clupeaformis*) and Least Cisco Complex (*Coregonus sardinella*).

Conspecific populations across Beringia

Round Whitefish *Prosopium cylindraceum* (Salmoniformes)

The Round Whitefish *Prosopium cylindraceum* occupies three separate regions. The Arctic and Atlantic drainages in eastern North America from Labrador

to Connecticut, Pacific and Atlantic drainages from northern British Columbia through Alaska to Western Hudson Bay, and the Asian Arctic (Page and Burr 1991). This species inhabits lakes and rivers and also is known to exhibit a variety of life histories—fluvial, adfluvial, anadromous and lacustrine—and may enter brackish waters (Bendock 1977; Bryan and Kato 1975; Koelz 1929; Kra'sikova 1968; Morin et al. 1982; Normandeau 1969).

Broad-scale phylogeographic study of this species across North America has recently been conducted revealing genetic structuring relating to survival in at least two glacial refugia in North America (Morgan 2016; Morgan et al. 2018). The southern range extent of Round Whitefish overlaps with the northern distribution of Mountain Whitefish (*Prosopium williamsoni*), and it is theorized that Round Whitefish did not colonize further due to competing with Mountain Whitefish populations already established in the Liard River drainage and southward (Guin 1982). Despite some geographical sympatry between these two congeners, no evidence of hybridization exists (Guin 1982).

Morgan (2016) and Morgan et al. (2018) included a single Eurasian sampling location of three individuals (Taniorer River, 66.154722, 175.762222) far outside West Beringia. These three samples; however, are noted by Morgan et al. (2018) to be substantially different in terms of mitochondrial sequence identity (on average 1.75%) and may warrant identification as a separate species. A single sequence of cytochrome b is available from the Lena River basin near Lake Baikal (Sukhanova et al. 2012: 57.033333, 108.600000) and is approximately 3% divergent from North American Round Whitefish mitochondrial haplotypes.

Prosopium species diversity is very limited outside North America. Aside from the Round Whitefish, the Pygmy Whitefish *P. coulteri* is documented only in the Amguema River basin from four lakes (Chereshnev and Skopets 1992; see specific section in this manuscript). Thus, characterizing Round Whitefish diversity and phylogeography in the context of Beringia is critical for further understanding post-glacial dispersal of coregonine fishes and species-level diversity in the region.

Inconnu *Stenodus leucichthys* (Salmoniformes)

Inconnu are known colloquially as sheefish, nelma, coney and have other regional names. The species is widely distributed, from the Kola Peninsula on the White Sea to Anadyr in Eurasia, rivers of Western Alaska including the Kobuk, Selawik, Yukon, and Kuskokwim, and the Mackenzie and Anderson rivers of Northwest Canada (Alt 1988; Chereshnev et al. 2000; McPhail and Lindsey 1970; Nikol'skii 1954). Inconnu is most commonly classified as two subspecies, a Caspian Sea form (*Stenodus leucichthys leucichthys*) that is bound within that basin, and the more widely distributed form across the rest of the species' range (*Stenodus leucichthys nelma*) (McPhail and Lindsey 1970; Nikol'skii 1954; Scott and Crossman 1973; Walters 1955).

Migration is a key aspect of Inconnu biology, with adults undertaking long upstream migrations to spawning habitats. Post-spawning downstream migrations are typical, and Inconnu may or may not enter estuarine habitats after spawning and over the course of their lifetimes (Alt 1987; Brown et al. 2007; Howland et al. 2001; Reist and Bond 1988; Underwood 2000). Inconnu populations have declined in certain parts of their range because of excessive exploitation (Chereshnev et al. 2000; Tallman and Holwand 2017) or large dams blocking upstream and downstream migrations (Dyubin 2007; Letichevsky 1981; Petrova 1976). Inconnu populations in some dammed drainages persist only through hatchery production (Dyubin 2007; Freyhof and Kottelat 2008a, b; Petrova 1976). Inconnu often utilize estuarine and coastal habitats across a broad range of salinities (e.g. Chereshnev et al. 2000; Howland et al. 2001, 2000; Petrova 1976; Smith and Sutton 2015) and may migrate over 100 km following coastal estuarine bands to access feeding habitats in brackish lagoons or other nearby river systems (Alt 1987; Fraley et al. 2022; Reist and Bond 1988). In an extreme case, an Inconnu that was tagged in the Kuskokwim River in southwest Alaska was recaptured five years later in the Yukon River, a feat requiring a coastal migration of approximately 500 km (Alt 1987). Migratory distances of some Inconnu within the Yukon and Mackenzie River drainages from estuarine habitat near river mouths to upstream destinations may span as much as 1700 to 1800 km (Brown 2000; Brown et al. 2007; Stephenson et al. 2017).

Morphological studies have not demonstrated differences between East and West Beringia (Walters 1955), e.g. between samples from the Ob River (Siberia) and Yukon River (Alt 1969; Chereshev et al. 2000; McPhail and Lindsey 1970). In Arctic Canada, anadromous Inconnu are well-characterized alongside freshwater Inconnu that are also migratory, (e.g. Howland et al. 2001). These fish show an ability to tolerate up to 25‰ salinity after acclimatization, and up to 15‰ without acclimatization. Thus, Inconnu are capable of colonizing new streams or moving among existing populations utilizing brackish nearshore environments.

Genetic studies involving Inconnu have been focused primarily in a phylogenetic context with a limited number of population genetic studies focused on specific fisheries-related questions at small spatial scales (Hander et al. 2017; Miller et al. 1998; Wiens 2018). A population genetics study of Inconnu in Alaska based on 20 microsatellites demonstrated genetic clustering in line with three regional groupings—the Yukon River, the Kuskokwim River, and the Kobuk and Selawik rivers in Kotzebue Sound (Olsen et al. 2017). Subdivision among spawning populations within the Yukon River were apparent between lower and middle river populations. A recent study of Inconnu population genetics using microsatellites in the Mackenzie River and the Great Slave Lake identified five genetic clusters of Inconnu, one in the Mackenzie River and four in the Great Slave Lake region (Wiens et al. 2021). These findings indicate that each river flowing into Great Slave Lake has a genetically distinct population with lower genetic diversity in those populations compared to the Mackenzie River. Howland (2005) detailed evidence supporting the hypothesis that Mackenzie River Inconnu originated from a Yukon River source population via headwater transfer near the end of the Wisconsin glacial period. Kotzebue Sound drainages that currently support Inconnu populations were glaciated during the Wisconsin glacial period (Elias and Brigham-Grette 2013) indicating a recent colonization event. Similar to the Mackenzie River, the most likely source population for the Kotzebue Sound streams would be from the Yukon River refugia, which would entail a relatively short coastal migration and would not require an extended open sea migration. Inconnu are currently present in the Anadyr River in West Beringia (Chereshev et al. 2000; Petrova 1976)

although it is not clear that the drainage supported Inconnu during the Wisconsin glacial period. Western Beringia is thought to have experienced substantial glaciation during the Wisconsin glacial period within the Anadyr River drainage and both north and south of what is now the Gulf of Anadyr (Elias and Brigham-Grette 2013). Other populations in Asia from large northern rivers such as the Kolyma River would require a much longer dispersal path than the Yukon River to colonize either the Anadyr River or Kotzebue Sound streams (Chereshev 1993). Following paleoriver drainages (Fig. 1), it is likely that the Anadyr River and Western Alaska populations of Inconnu are more closely related to each other than the Anadyr River and Northern Asian populations, but this remains to be tested. Given the migratory ability of Inconnu, evaluating historic versus contemporary connections to assess any similarity of Anadyr River and Alaskan fishes should be undertaken.

Notably, hybrids between Inconnu and Humpback Whitefish (*Coregonus clupeaformis*; Lake Whitefish Complex) have been observed in the Yukon River in Alaska and the Anderson River estuary in northern Canada (Alt 1971; Brown et al. 2012; Reist et al. 1992). Being broadcast spawners, coregonines are thought to hybridize among closely related species that spawn in similar habitats at similar times rather than intentional pairing between species. The frequency and role of hybridization of Beringian whitefishes remains poorly evaluated.

Broad Whitefish *Coregonus nasus* (Salmoniformes)

Unlike many other species in the genus *Coregonus*, the Broad Whitefish exhibits very little taxonomic ambiguity (Lindsey, 1962), is easily identified across its range, and is genetically distinctive (e.g. Bernatchez et al. 1991; Bodaly et al. 1991; Politov et al. 2000, 2004). Broad Whitefish inhabit Arctic drainages from Volonga, Russia (46° E) eastwards through Alaska and into Arctic Canada (102° W) (Freyhof and Kottelat 2008c). Broad Whitefish are also present in several Bering Sea drainages from the Kuskokwim River northwards in East Beringia (Alt 1976; Harper et al. 2012; McPhail and Lindsey 1970). In West Beringia the species distribution in the literature indicates the Anadyr River, and may include a distribution south to the Bay of Korf on the Kamchatka Peninsula and rivers of the northern Sea of Okhotsk

such as the Penzhina River (McPhail and Lindsey 1970; Shestakov 2001). The species is also found in rivers, lagoons, and other brackish estuary habitats in Alaska along the Beaufort and southern Chukchi Sea coastlines (Craig 1984; Fraley et al. 2022; Georgette and Shiedt 2005; Priest et al. 2018; Reist and Bond 1988).

Like many other whitefish species, the Broad Whitefish exhibits a wide diversity of life history variation. Throughout their range, Broad Whitefish occupy large and small rivers, migrate into accessible lake systems to feed and sometimes overwinter, and while some populations remain in freshwater throughout their life, other populations migrate to sea to forage in estuaries and coastal lagoons (Brown et al. 2007; Harper et al. 2012; Harris et al. 2012a; Reist and Bond 1988; Shestakov 2001; Tallman et al. 2002). Many of these life history and population affiliation details have come to light in recent decades with the use of new technologies such as radio telemetry (Carter III 2010; Harper et al. 2012; Millar et al. 2013), otolith chemistry (Brown et al. 2007; Harris et al. 2012a; Leppi et al. 2021), and genetics techniques (Bodaly et al. 1991; Harris et al. 2012a; Harris and Taylor 2010; Politov et al. 2000).

Phylogeographic studies of this species have largely failed to provide representative sampling of both East and West Beringia in the same study (e.g. Ermolenko 1991; Harris and Taylor 2010). Harris and Taylor (2010) provide a detailed analysis of East Beringian populations of Broad Whitefish and included several Canadian Arctic populations. Harris and Taylor (2010) conclude that this species survived through glacial episodes in the Beringian refugium and dispersed post-glacially to reach its current distribution using both marine and freshwater mediated means. However, it is unclear if Broad Whitefish reached the Mackenzie River via a headwater transfer from the Yukon River, or, if the species persisted in the Arctic Coastal Plain and dispersed via brackish water transfers into the Mackenzie drainage. A single location from Eurasia was included by Harris and Taylor (2010), a distance of approximately 3470 km from the other locations in their study. Given the extremely large range of this species, the genetic distinctiveness of this sample from others was not surprising (Harris and Taylor 2010). Importantly, due to the large geographic distribution of the species, the genetic structuring that does appear to exist across Siberia, at least

a broad East–West division which should be considered in future studies examining this species. Doing so would more accurately characterize the role of Beringia’s changing environment in the distribution and survival of Broad Whitefish.

The genetic distinctiveness of life history variants in Broad Whitefish when examined in Arctic Canada (Harris et al., 2012b) suggested that there is a heritable component to the behavior. If so, to what extent is the same adaptive genetic variation utilized between the similar life history variants in different locations? Do East and West Beringian anadromous Broad Whitefish utilize the same basic genetic variants, or, has the same phenotype arisen from perhaps the same pathways, but with alternative genetic alterations? What are the epigenetic contributions to life history variation in this species? Answering these questions would not only address long-standing questions in evolutionary biology (e.g. Orr 2005), but may extend scientific understanding on the way in which Beringian fish transitioned to various life histories after dispersing from refugia.

Arctic Cisco *Coregonus autumnalis* (Salmoniformes)

The Arctic Cisco *Coregonus autumnalis*, referred to as ‘Omul’ in Russia, is a widely-distributed anadromous species found in most large Arctic drainages and associated estuaries in Eurasia from the Mezen’ River on the White Sea in the west to the Kolyma River in the east, including the Pechora, Yenisei, Khatanga, Lena, Indigirka, and Kolyma rivers (Moskalenko 1971; Nikol’skii 1954). In North America the species is found in coastal waters from Utqiagvik (formerly Barrow; 156.7° W) to Coronation Gulf (112° W; McPhail and Lindsey 1970; Mecklenburg et al. 2002). Phylogenetically, the Arctic Cisco is closely related to *C. pollan* of Ireland, *C. artedi* of Eastern North America, and *C. laurettae* in western Alaska Supplemental Figure S1 (Crête-Lafrenière et al. 2012; Ferguson et al. 1978; Politov et al. 2004; Turgeon and Bernatchez 2003). While the population of *C. pollan* is disjunct from the natural range of Arctic Cisco it is genetically very similar and has been considered by some to be a subspecies (*C. autumnalis pollan*; Ferguson et al. 1978). The distributions of Arctic Cisco and Bering Cisco intersect in the western Beaufort Sea (Bickham et al. 1997; McPhail 1966).

Arctic Cisco in Beringia originates from only a small number of spawning locations. Fish captured in Beringia are from spawning populations in the Kolyma or Indigirka Rivers in Eurasia and the Mackenzie River in North America. In North America, the only known spawning population occurs in the Mackenzie River, resulting in fish distributed some 650 km westward of their origin (e.g. Dillinger et al. 1992; Fechhelm et al. 2007; Moulton 1989; Zimmerman et al. 2013). Genetic and otolith microchemistry study of Arctic Cisco collected in the Colville River is consistent with a Mackenzie origin of the fish (Zimmerman et al. 2013).

We evaluated mitochondrial diversity in Arctic Cisco assessed through available COI sequences in Genbank (n=33). Both Eurasian and North American representatives of Arctic Cisco were available, and indicate a high degree of overall genetic similarity in terms of mitochondrial haplotypes (Politov et al. 2004). One sequence (KP452507) is divergent from Arctic Ciscos and is placed within the Lake Whitefish complex and most likely a misidentification. A single sequence available from *C. pololan* (JX960898.1) is nested within the Arctic Cisco sequences when compared to all sequences and is very similar (up to 100% identical), see Supplemental Figure S1. Given the geographic divergence between the West and East Beringian Arctic Ciscos, three questions remain to be clearly assessed (1) When did Asian and North American fish separate? (2) Is there currently any gene flow of Arctic Ciscos across Beringia? (3) Following these questions, should Beringian Arctic Cisco be treated as one or more species?

Predominantly North American species with Asian isolates

While Pygmy Whitefish and Bering Cisco share a general pattern of being widely distributed in North America with few populations or individuals identified in West Beringia, there are key biological differences. The Pygmy Whitefish is a small, short-lived, freshwater species with no evidence of anadromous capacity. However, the observations of the species in four lakes in the Amguema River in west Beringia (Chereshnev and Skopets 1992) indicates that a crossing, most likely from East to West Beringia, took place at some point. Because Pygmy Whitefish are similar in appearance to juvenile Round Whitefish,

and sampling often entails unique challenges of depth and gillnet mesh size, it is likely that more populations will be discovered with greater focused effort (Blanchfield et al. 2014; Vecsei and Panayi 2015).

Bering Cisco *Coregonus laurettae* are anadromous and widely distributed in coastal environments in western Alaska and in Cook Inlet (Alt 1973; McPhail 1966; Padilla et al. 2016), while in West Beringia only two individuals have been documented feeding in an estuary of the Chegitun' River, just north and west of the Bering Strait (Chereshnev 1984). Chereshnev (1993) suggests that this rare species may be present elsewhere in that area of the Chukotka Peninsula but no additional individuals have been documented and no spawning runs have been identified. Because of their affinity for marine environments, it is possible that the few Bering Cisco captured in the estuaries in West Beringia have natal origins in western Alaska and migrated across the Bering Strait. The few individuals identified in Asia are not strongly indicative of a spawning population.

Pygmy Whitefish *Prosopium coulteri* (Salmoniformes)

Discussed previously.

Bering Cisco *Coregonus laurettae* (Salmoniformes)

Bering Cisco *Coregonus laurettae* is an anadromous species with a terminal mouth and pale ventral fins (Bean 1881) that was at one time considered synonymous with Arctic Cisco in North America (Dymond 1943; Walters 1955). It was eventually discovered that Bering Cisco are morphologically distinct from Arctic Cisco based most clearly on lower limb gill raker counts of 21–25 compared to 26–30 for Arctic Cisco (McPhail 1966) and North American Arctic Cisco are synonymous with Asian Arctic Cisco *Coregonus autumnalis*. Subsequent genetic study has supported a close, but independent relationship between Bering Cisco and Arctic Cisco (Bernatchez et al. 1991; Crête-Lafrenière et al. 2012; Politov et al. 2004; see also Supplemental Figure S1).

The Bering Cisco migrates to sea during its first year and disperses widely in coastal and near-coastal habitats in the Gulf of Alaska, eastern Bering Sea, the Chukchi Sea and into the Beaufort Sea near the Colville River (Alt 1973; McPhail 1966; Padilla et al.

2016). This species has been observed in coastal habitats of Northwest Beringia but no known spawning population has been observed there (Chereshnev 1984). The spawning locations of this species are restricted both in terms of the river basins and the habitats used for spawning (Brown and Daum 2015; Brown and López 2018). While Bering Cisco spawning areas have been observed in the Yukon, Kuskokwim, and Susitna rivers, they occur in braided mainstem regions of these drainage basins (Brown and Daum 2015; Padilla et al. 2015; Russ 2015). Both otolith chemistry and genetic study has supported the distinctiveness of the three known spawning populations and no data have suggested that additional populations exist (Padilla et al. 2015; Russ 2015). Genetic and morphological analyses are consistent in demonstrating a closer relationship between Yukon and Kuskokwim River spawning populations than between those populations and the Susitna River population (Brown and López 2018; Russ 2015).

Evidence to date supports the hypothesis that during the last glacial episode, Bering Cisco were able to survive in either one or both of the unglaciated Yukon and Kuskokwim paleorivers (Elias and Brigham-Grette 2013). At the end of the LGM, Bering Cisco may have colonized the Susitna River, which had just emerged from under glacial cover, via the ocean or headwater transfer (Brown and López 2018). This species did not successfully colonize the Anadyr River in West Beringia (Chereshnev 1993), which given its migratory tendencies and salinity tolerance (Padilla et al. 2015) may have been possible. The presence of this species in West Beringia does lead to several questions that could be informed by otolith microchemistry and/or genetic study of fish from West Beringia. If there is in fact no spawning population in West Beringia, then we could infer that the Bering Cisco is capable of crossing the Bering Sea from the mouths of Yukon and Kuskokwim Rivers at least over to the Northern Chukchi Peninsula. The lack of spawning populations in West Beringia may be related to a high fidelity to spawning grounds (Padilla et al. 2015). Alternatively, if there is a spawning population of Bering Cisco in West Beringia, it would be only one of four known spawning locations of this species. Important questions would be raised by such a finding. When was it established? What are its genealogical relationships? How does this information reform the current hypothesis of a

Yukon-Kuskokwim refugium survival and post-glacial expansion of this species?

Species complexes

Lake Whitefish Complex *Coregonus lavaretus*, *C. clupeaformis*, *C. muksun*, *C. nelsonii*, *C. pidschian*, *C. anaulorum* (Salmoniformes)

The Lake Whitefish Complex exhibits a very wide distribution, from Western Europe to Eastern North America. As such, a great many taxonomic names may be included under this umbrella outside Beringia, and the names listed under this heading are not complete for the complex. *Coregonus lavaretus* itself may be narrowly defined to occupy Lakes Bourget and Geneva in France and Switzerland (Fricke et al. 2021); however, the name *lavaretus* has been widely applied to North American and Siberian whitefishes. Within Beringia, the Humpback Whitefishes—*C. clupeaformis*, *C. muksun*, *C. nelsonii*, *C. pidschian* should be addressed as members of the Lake Whitefish Complex.

Overall, the Humpback Whitefishes exhibit close genetic relationships, and while they may exhibit morphological differences, genetic distinctions between them are not pronounced (Supplemental Figure S1). One approach to binomial nomenclature is to apply the species name *C. lavaretus* to all Humpback Whitefishes across Europe, Asia and North America as they are similar in genetic and morphological composition (Bernatchez and Dodson 1994). Alternatively, *C. clupeaformis* may be applied to North American forms of Humpback Whitefish, (e.g. McDermid et al. 2007); though the Beringian-type Humpback Whitefish do cross between continents and *clupeaformis* may be considered a name useful to apply to *pidschian*-like fish of West Beringia. Nevertheless, McDermid et al. (2007) did not extend their analysis across the Bering Strait from North America highlighting the need for the integration of data sets across Beringia to resolve questions of the distribution of *C. clupeaformis* if that name is applied to Humpback Whitefish in North America.

While there are diverse anatomical forms within the Lake Whitefish Complex that appear to originate from the same species-wide standing genetic variation, in West Beringia, what underlies the apparent

anatomical differentiation between Muksun *C. muksun* and other Humpback Whitefish requires further investigation. While anatomically distinctive, genetic investigations to date with allozyme and mtDNA markers have not identified diagnostic genetic traits and *C. muksun* is sympatric with other members of the Lake Whitefish Complex (e.g., Baldina et al. 2008; Politov 2017; Politov et al. 2000, 2004). However, genetic investigations have shown the presence of allozyme alleles and mtDNA haplotypes within some *C. muksun* that are typical of the Least Cisco Complex (Fleischer 2002; Politov et al. 2000). This evidence points to a hybrid origin of *C. muksun* that remains incompletely tested along with the question of multiple origins of *C. muksun* through hybridization in different drainage basins (Baldina et al. 2008).

We include the Sharpnose Whitefish *C. anaulorum* in this section as it has close affinities to the sympatric Lake Whitefish Complex but is morphologically and ecologically distinct. Furthermore, while differentiation is not detected with allozymes between Sharpnose Whitefish and Humpback Whitefish, evidence indicates the presence of two divergent mtDNA lineages in the sympatric fishes of both types (Ermolenko 1989; Politov 2017). One of these lineages present in Sharpnose Whitefish is typical of Humpback Whitefish and the other is similar to *Coregonus* mtDNA lineages found in the Baikalian rift zone. Thus, a history of hybridization with an otherwise unrepresented *Coregonus* lineage appears to underlie the origin of Sharpnose Whitefish. Technological and analytical advances have allowed the characterization of hybridization with archaic populations or sister lineages that are now extinct, and the role of such hybridization in evolution has been highlighted as important in Humans and in Killer Whales *Orcinus orca* (e.g., Foote et al. 2019; Racimo et al. 2015; Skov et al. 2018). The testing for ancestral hybridization with an extinct species in the origin of Sharpnose Whitefish may now be explored with contemporary techniques and contribute greatly to understanding the origins of coregonid diversity.

Least Cisco Complex *Coregonus. albula*–*C. peled*–*C. sardinella*—*C. subautumnalis* (Salmoniformes)

The distribution of this complex is from Western Europe into Western North America with the two most-widely distributed types—the Vendace (*C.*

albula) and the Least Cisco (*C. sardinella*)—overlapping at the Pechora River in Northwest Russia. Within the Pechora River system the ecological preferences for the species is shown through the Vendace inhabiting lakes and small tributaries while the Least Cisco occupies the main river habitat (Sendek 1998). The composition of the Least Cisco Complex has been substantially modified based on molecular research reviewed by Politov et al. (2017), leading to the realization that Peled (*C. peled*, formerly placed with Arctic Cisco, Amur Whitefish *C. ussuriensis* and Tugun *C. tugun*) and the Penzhina Cisco (*C. subautumnalis*, formerly considered a close relative of Arctic Cisco) are members of the Least Cisco Complex (Supplemental Figure S1).

Within Beringia, the Least Cisco appears to be the sole member of the complex but its diversity in terms of life history, ecotypes and population genetic structuring are poorly known across its range, which extends from the Anadyr River in West Beringia, St. Lawrence Island in the northern Bering Sea, coastal environments in East Beringia from Bristol Bay north, throughout the Yukon and Kuskokwim rivers, across the Arctic coast to Cambridge Bay in the Canadian Archipelago, and up the Mackenzie River and into the Great Slave Lake (Brown et al. 2007; McPhail and Lindsey 1970; Moulton et al. 2010; Muir et al. 2014). Least Cisco populations are highly adaptable and capable of many different life history strategies including riverine and lake-resident types, anadromous and freshwater forms, and large and dwarf forms (Brown et al. 2007; Craig 1984; Lindsey and Kratt 1982; Mann and McCart 1981; Muir et al. 2014). Thus this wide-ranging species is subject to diverse selection pressures across a variety of habitats and latitudes (e.g. Padula et al. 2017). Research in West Beringia has resulted in the resolution of relationships of Least Cisco with members of the Least Cisco Complex outside of Beringia (e.g. Bodaly et al. 1991, 1994). There is one study of East Beringian Least Cisco mitochondrial phylogeography that indicates at least three broad-scale phylogeographic groupings of Least Cisco and a surprisingly high degree of mtDNA haplotype diversity similar to Alaska Blackfish in East Beringia (Campbell and López 2014; Padula et al. 2017). The three broad-scale phylogeographic groupings identified by Padula et al. (2017) are broadly Arctic Coastal Plain, Northwest Alaska, and the Yukon-Kuskokwim Basin.

There remain several important questions in Beringia about the Least Cisco Complex. Research has continued to indicate that there are anadromous, riverine and lake resident ecotypes, but the distributional records are widespread. The occurrence of Least Cisco in intermediate areas is inferred, some lake populations in southwest Alaska appear to be isolated, and the abundance of Least Cisco in many areas is unclear as reviewed by Brown et al. (2012). Neutral genetic study can identify to what degree West and East Beringian Least Cisco populations are connected and if phylogeographic divides evidenced in East Beringia translate across the Bering Strait leading to stronger trans-Beringian relationships as opposed to North–South divisions within East Beringia. As the characterization of anatomical and ecotypic diversity of Least Cisco improves, the evolutionary origins and interplay of diverse Least Cisco forms may be informed through characterization of genomic diversity.

3.0 Amphidromous and Anadromous Fishes

Arctic Lamprey Complex *Lethenteron* spp.
(Petromyzontiformes)

Anadromous and resident populations of species of Arctic Lamprey (*Lethenteron* spp.) are found broadly across Beringian drainages. Evidence from mtDNA sequences suggest that the three putative species of *Lethenteron* found in Beringia (i.e. *L. alaskense*, *L. camtschaticum*, *L. kessleri*) form a group of poorly differentiated lineages with questionable species status (e.g. Artamonova et al. 2015; White 2014). Here we treat these three nominal forms together as the Arctic Lamprey Complex.

Populations from the Arctic Lamprey Complex are known from between the Amur and Ob river drainages to the south and west, respectively, across the Bering Sea and the Mackenzie River drainage to the east (Renaud 2011). In North America, Arctic Lamprey have also been recorded in coastal rivers of the North Pacific and of the western Chukchi Sea on the northwestern coast of Alaska (Mecklenburg et al. 2002). Life history diversity among species and populations of lamprey in general and Arctic Lamprey in particular pose an interesting challenge and opportunity for biogeographic research. Anadromous and

freshwater resident species and/or populations of lamprey are found in sympatry broadly across their range. Freshwater resident populations likely originate as life history variants of anadromous populations that colonize habitats suitable for the resident life history strategy, which bypasses an extended phase of substantial growth in the marine environment. Determining whether sympatric populations showing alternative life history strategies are genetically distinct will be an essential component of identifying historical connections and understanding the evolution of the distribution of Arctic Lamprey diversity in Beringia. The reliance on morphology for defining Lamprey species has led not only to the partition of life history variants into separate species, but also to overlooking cryptic species (Auringer et al. 2023; Boguski et al. 2012). This has been especially apparent in Western North America, and study of Beringian Lamprey at a basic taxonomic level is needed.

Within Beringia, the Arctic Lamprey Complex currently occupies areas that would have been part of Arctic and North Pacific Ocean drainages during high-glacial extent and low-sea level periods. Documented patterns of present abundance of Arctic Lamprey in the marine phase in the Bering Sea and North Pacific shows two centers of higher abundance in the northeastern Bering Sea and the western Sea of Okhotsk (Orlov et al. 2014) becoming much less abundant but broadly present along waters of the Arctic coasts of Asia and North America (Novikov and Kharlamova 2018). Based on these observations we consider two alternative biogeographic scenarios for the present distribution of Arctic Lamprey. Arctic Lamprey populations currently found in Arctic-draining systems are of relatively ancient and independent origin. Under this model, the potential connectivity to populations outside the Arctic via the Bering Sea has had minor to no effect in the genetic composition of Arctic populations. Alternatively, the Bering Sea has been and is an important channel for dispersal, range evolution, and connectivity among Beringian Arctic Lamprey populations. Under this scenario, genealogical differentiation is primarily dictated by relative proximity among spawning sites independent of historical drainage patterns.

Pond Smelt *Hypomesus olidus* (Osmeriformes)

The species occupies several disjoined areas and exhibits freshwater and anadromous ecotypes. Within western Beringia, Siberian Pond Smelt (*H. olidus*) are found 2500 km from other populations in the Kara Sea (McPhail and Lindsey 1970). In East Beringia the species is not found on the Arctic Coastal Plain, while present in the Yukon Territory (Canada) and Mackenzie River. This represents a distance of > 1100 km from the Kobuk River in northwestern Alaska (Degraaf 1986). Found in Western Alaska and the Alaska Peninsula, the species again is found in Southeast Alaska southwards through Western British Columbia to Central California (Saruwatari et al. 1997). Recently, a predominantly freshwater population was identified on Bering Island (Malyutina et al. 2017), and the species is found westward to Korea and Hokkaido.

While subject of recent phylogenetic study with both Eurasian and North American populations examined (Ilves and Taylor 2007) and surveys of genetic diversity have occurred with mtDNA in Eurasia (e.g. Skurikhina et al. 2012), much of the eastern part of the range has not been subject to genetic study and examination of populations in the context of Beringia. Given the widely separated sub-ranges of this species, taxonomic uncertainty of the genus, as well as the propensity to form freshwater resident populations, further study to examine speciation and trans-Beringian connections is warranted.

Pacific Rainbow Smelt *Osmerus dentex* (Osmeriformes)

Revision of *Osmerus* has led to three species being recognized in this circumpolar genus (Taylor and Dodson 1994): The European Smelt (*Osmerus eperlanus*) found in the North Atlantic eastward into the Barent's Sea, the Rainbow Smelt (*O. mordax*) of the Northwest Atlantic and the Pacific Rainbow Smelt (*O. dentex*) of Alaska, Primorski Kray, Kara's and Barent's Seas. Molecular evidence indicates that the Pacific Rainbow Smelt and European Smelt are sister lineages (Ilves and Taylor 2009), but no trans-Beringian molecular studies for the Pacific Rainbow Smelt has been conducted. Rainbow Smelt (*O. mordax*) was noted by Lindsey and McPhail (1986) to not be a species with trans-Beringian morphological distinctions,

which now would apply to Pacific Rainbow Smelt. In the West Beringian segment of the range, molecular study has not shown large biogeographic divisions in Pacific Rainbow Smelt (Kovpak et al. 2011) and this species appears to lack ecotypes found in Rainbow Smelt (e.g. Taylor and Bentzen 1993).

The Arctic Charr Complex *Salvelinus alpinus*, *Salvelinus boganidae*, *Salvelinus elgyticus*, *Salvelinus confluentus*, *Salvelinus malma*, *Salvelinus taranetzi*, *Salvethymus svetovidovi* (Salmoniformes)

There exist several species of *Salvelinus* that are closely-related and are discussed under the concept of an Arctic Charr species complex (Taylor 2016). This Arctic Charr species complex may also contain the Long-Finned Charr (*Salvethymus svetovidovi*) currently placed into a monotypic genus. The Lake Trout discussed previously, is clearly distinct from these species phylogenetically and biologically and should not be considered part of the complex. The Arctic Charr complex was reviewed fairly recently by Taylor (2016), with a general conclusion that the taxonomic diversity of these charrs across the Pacific is not well understood and requires comprehensive geographic sampling and transboundary cooperation to resolve.

Threespine Stickleback *Gasterosteus aculeatus* (Gasterosteiformes)

The Threespine Stickleback (*Gasterosteus aculeatus*) is a widespread species in the Northern Hemisphere and exhibits marine, anadromous and freshwater ecotypes. The freshwater ecotypes are generally thought to derive independently from marine and anadromous ancestry (McPhail and Lindsey 1970). Range-wide phylogeographic study of this species broadly indicates two mitochondrial clades, one characteristic of Europe and North America and another distributed around Japan estimated to have diverged 0.9–1.3 million years ago (Ortí et al. 1994). In South-central Alaska, the presence of both mitochondrial clades was found by Ortí et al. (1994), with the Japanese clade found only in freshwater lakes. Additional sampling of Western Alaskan and Eastern Russia revealed widespread presence of the Japanese clade in coastal samples (Chythlook 2000).

While Chythlook (2000) expanded sampling within Beringia for the Threespine Stickleback, the

sampling locations, as with Ortí et al. (1994) focused on coastal populations, not interior freshwater populations. Examining inland populations of this species at a greater resolution within Beringia that may have survived in isolation would advance our understanding of the persistence of this species through the glaciations of the Pleistocene.

Ninespine Stickleback *Pungitius pungitius* (Gasterosteiformes)

The Ninespine Stickleback (*Pungitius pungitius*) is a circumpolar species of stickleback that is distributed more northerly and with more predilection for freshwater habitats compared to the Threespine Stickleback (Wootton 1976). The Ninespine Stickleback is capable of utilizing a broad range of environmental conditions and may undergo spawning migrations, nonetheless it is more abundant in freshwaters compared to marine waters (e.g. Arai and Goto 2005, 2008; Ovajeer et al. 2000).

Previous anatomical study indicated two distinct forms across the North American range of this species with a hypothesis of origin from two distinct refugia—Beringian and Mississippian—with no morphological differences noted between East and West Beringia (Lindsey and McPhail 1986; McPhail 1963). A broad phylogeographic study of the species utilizing mitochondrial loci and microsatellites sampled East Beringia (Seward Peninsula and the Cook Inlet region of Southcentral Alaska) but omitted West Beringia (Aldenhoven et al. 2010). Aldenhoven et al. (2010) did recover two distinct genetic groupings compatible with the Beringian and Mississippian refugial origins of McPhail (1963) but also several other distinct phylogeographic units. Thus, it is still unclear if there is a significant divide within Beringia phylogeographically for this species on a North–South or East–West axis. In the European segment of the range of this species, colonization from two distinct freshwater populations is indicated by genetic study (Shikano et al. 2010), thus, despite the ability for this species to enter marine waters, substantial divergence may be present within Beringia owing to persistence in freshwater sub-refugia.

Discussion

Comparison of Beringian fish phylogeography clearly indicates that different species survived glaciations and colonized available habitat post-glaciation in unique ways (e.g. Bernatchez and Wilson 1998). There are several conclusions that may be drawn from the current information available and there remain several open questions for different species and species complexes that until resolved prevent a final broad characterization of Beringian fish phylogeography.

Salient characteristics of Beringian fish phylogeography

Across the two major geographic axes, North–South and East–West, Beringian fishes exhibit alternative phylogeographic connections (Figs. 1 and 2). In general, there is a North–South divide and an East–West connection leading to closer relationships across the Bering Sea than across the Brooks Range in Alaska or North and South Chukotka. Historical connectivity through the Chukchi Sea, Anadyr Gulf, and Yukon–Kuskokwim paleorivers is likely a driver of these patterns. These historical connections have led to close relationships within Beringia among fish species.

While paleorivers may lay the foundation for consistency among Beringian freshwater fish species in terms of phylogeography, there is clearly a high degree of stochasticity in the survival of species and genotypes in the region that individual species biology contributes to. For example, the Lake Trout has long been present in East Beringia, with no evidence of ever crossing the Bering Strait. The preferred habitat of Lake Trout in Beringia is found now where there were glaciers and ice fields historically, and there was not comparable habitat extending across the Bering land bridge that would permit trans-Beringian dispersal. Lake Chub and Trout-Perch, on the other hand, inhabit waterways that should allow dispersal between East and West Beringia through paleorivers, yet, these species remain found only in East Beringia. Longnose Sucker is found in both East and West Beringia, but is not found on the Chukotka Peninsula (for further discussion of odd distributions, see Lindsey and McPhail 1986). The current distributions and genealogies of Beringian freshwater fishes are

influenced by stochastic factors and species biology; however, there is still evidence of shared factors.

How do Beringian fish survive?

Logically, isolated specialists are prone to extinction in dynamic environments. The paleoclimatic instability of the Pleistocene in some ways aided intercontinental exchange of species raising diversity east and west of the Bering Strait, but at the same time paleoclimatic instability decreased species diversity within Beringia. Species diversity in the world follows a well-known latitudinal gradient of species richness where species diversity is highest at the equator and declines towards both poles (e.g. Hillebrand 2004; Humboldt 1828). While there is an expectation for low species diversity in Beringia, there is certainly occupation of a diverse suite of freshwater fishes across Beringia and in terms of biomass, fishes are not sparse. Looking forward with a continually changing and dynamic environment in Beringia, identifying how freshwater fishes survived and making sure those methods are not interrupted will ensure long-term survival of freshwater fishes in Beringia.

Low genetic diversity in small populations

A long-standing paradigm is that genetic diversity is a key component of survival of organisms. Populations also need to maintain a certain number of individuals to overcome demographic stochasticity, where loss of a few individuals may have a disproportionate impact on population viability. Small populations are subject to drift, inbreeding and demographic stochasticity, and therefore are considered to be limited in terms of adaptive potential and ability to persist. The 50/500 rule was proposed to provide some guidelines. Those populations with an inbreeding effective population size < 50 are at immediate risk of extinction, while a variance effective size < 500 indicates a population is at a long-term risk of extinction (Franklin 1980). Overall, standing genetic diversity is important for future adaptation (Barrett and Schluter 2008). While genetic diversity within Beringian freshwater fishes is comparatively lower and restriction to refugia has bottlenecked many species, they persist in a dynamic environment and have largely undergone post-glacial range expansion (Bernatchez and Wilson 1998).

Investigation of small populations has found overall that heritability does not decline along with population size until effective population size is very small ($N_E < 10$) (Wood et al. 2016). Wood et al. (2016) provide evidence that in the short term, small populations may still respond to selection. The concept of “propagule pressure” as in the number of founders, has been used as an explanation of the success of invasive species including their geographic spread (Lockwood et al. 2005). Those invasions starting with more founders can be hypothesized to be more successful. Another important consideration is biotic resistance, and in the case of post-glacial expansion from refugia, biotic resistance may be low as fishes are moving into habitats that have recently become available. Overall, there is evidence that abiotic environmental suitability is a larger determiner of invasive species success (e.g. Blackburn and Duncan 2001). With regard to fishes, salmonids and Northern Pike are typical Beringian fishes that may provide some insight into the ability of small populations to survive and expand into new habitats. Salmonids and Northern Pike have been distributed through human-mediated introductions and some inferences of past processes may be drawn from observations of these much more recent events.

The Kerguelen Islands are located in the Southern Ocean (49° S, 70° E) to which eight species of salmonids were introduced into previously fish-less freshwater systems (Lecomte et al. 2013). Brown Trout (*Salmo salar*) have been the most successful, and have invaded 32 watersheds systems beyond where they were introduced in 10 generations. Natural colonization through anadromous individuals contributed greatly to the spread of the species (Labonne et al. 2013). More detailed study of two populations artificially founded by a single female and one or two male parents in 1993 through collections in 2003 and 2010 demonstrates low genetic variation; however, the populations are successful (Labonne et al. 2013, 2016). Northern Pike are characterized by extremely low genetic variation, but are invasive in Alaska south of the Alaska Range presumably from introductions of a few individuals (Campbell et al., 2023). The first evidence of invasive Northern Pike is noted from 1950's and they have since spread and been introduced in more than one location from alternative source populations (Dunker et al. 2020). Recent genetic study of invasive Northern Pike populations

with high-throughput sequencing (RADseq) has further demonstrated that Northern Pike have very little genetic diversity with a mean heterozygosity of 0.036 in natural populations and 0.023 in invasive populations while being a very successful invasive species (Jalbert 2018). The known dates and locations of Northern Pike introductions and relative accessibility of sampling in Southcentral Alaska can provide insight into how Beringian fishes may have expanded their range from few starting individuals with limited genetic diversity.

In the context of the three major classes of fish discussed in the review, primary freshwater fishes, secondary freshwater fishes and amphidromous and anadromous fishes, low genetic diversity in small populations may play out differently as a result of several different factors. Dispersal ability and the ability to exchange migrants through coastal and marine habitats can bolster small populations both genetically and demographically, and fish not restricted to freshwater dispersal and connectivity, may be less subject to genetic bottlenecks as a result.

The splitting of populations across habitats with partially migratory fishes, where some individuals migrate and some do not within a population (Chapman et al. 2012), confers protection from stochastic events that may eliminate a portion of the population. Life history diversity acts to attenuate population fluctuations and reduce the impact of environmental fluctuations (e.g. Moore et al. 2014). A high degree of life history variability present across fish capable of entering saltwater, such as the Round Whitefish that exhibit adfluvial, fluvial, lacustrine and anadromous life histories, buffers this fish against serious declines across all habitats. Varying life histories incorporating habitats of different salinities are possible in secondary freshwater fishes and amphidromous and anadromous fishes. This variability acts to support demographic persistence of small populations, and may explain the dominance of migratory fishes in Beringia.

Adaptive introgression and hybridization

Utilizing standing genetic variation is a primary mode of adaptation in organisms (Barrett and Schluter 2008). While a particular population may have low levels of genetic diversity and not have on

hand adaptive genetic variation, another population of a closely related species or the same species may have variation present. Introgression of adaptive genetic variation can lead to rapid adaptation, as shown in *Fundulus* species where hybridization and introgression within the last 30 generations made evolutionary rescue from severe pollution possible with a single locus of large adaptive advantage (Oziolor et al. 2019). Adaptive introgression of a small genomic region from a single origin in Chinook Salmon (*Oncorhynchus tshawytscha*) has been shown to be the origin of the spring run phenotype across the range of this species (Prince et al. 2017; Thompson et al. 2020). Within Beringian fishes, there are known cases of hybridization, such as between Arctic Charr and Dolly Varden (Taylor et al. 2008; Taylor and May-McNally 2015), among *Coregonus* and *Stenodus* species, and within *Coregonus* (Alt 1971; Brown et al. 2012; Reist et al. 1992). However, what functional role that these hybridization events of Beringian fishes may have is unknown, particularly since the rates of hybridization, vigor and reproduction success of hybrid individuals have not been characterized. Hybrids have been recently observed between closely-related Arctic mammalian species and are presumed to be increasing with examples from whales “Narluga” Beluga (*Delphinapterus leucas*) x Narwhal (*Monodon monoceros*) hybrids and “Grolar”, “Pizzly”, or “Nanulak” Polar Bear (*Ursus maritimus*) x Grizzly Bear (*U. arctos*) hybrids (Pongracz et al. 2017; Skovrind et al. 2019).

There are at least three outcomes from hybridization that can be evaluated. One outcome is that hybridization between closely-related species increases genetic variation and consequently adaptive potential (e.g. Grant and Grant 2019). Secondly, hybridization can generate a hybrid taxon that utilizes an alternative ecological niche to the parental species as suggested by stable isotope evidence with the Narluga (Skovrind et al. 2019). Thirdly, for cases of co-occurring species that are ecologically differentiated but genetically similar like Polar and Grizzly Bears as well as *Coregonus* species, the species barrier may break down with sufficient disturbance, and hybridization leads to losses of ecotypic and species diversity (e.g. Grabenstein and Taylor 2018; Ortego et al. 2017).

In Beringian fishes, hybridization within primary freshwater fishes and the anadromous and

amphidromous fishes in this review is not notable. Hybridization of what are broadly secondary freshwater fishes, coregonines of the genera *Coregonus* and *Stenodus* is widespread, occurring at spawning grounds shared by these species. Commonly observed hybrids are Inconnu x Humpback Whitefish, Inconnu x Least Cisco and Humpback Whitefish x Least Cisco (e.g. Brown et al. 2012; Reist et al. 1992). Main *Coregonus* lineages date to the Miocene and appear to have undergone adaptive radiation in the Pleistocene in the Arctic along with the cooling and instability associated with that epoch. Given the close affinities of *Stenodus* with *Coregonus*, it may be included in this adaptive radiation. The formation of adaptive radiations relies on two components, divergent selection and reproductive isolation. The divergent selection resulting in diverse species of *Coregonus* and *Stenodus* is apparent, and introgression of genomic regions that increase adaptive potential and genetic diversity are known from adaptive radiations (Grant and Grant 2019). Evidence indicates that ancient hybridization events contributed to speciation in coregonines with the Sharpnose Whitefish and Muksun potentially of hybrid origin (Ermolenko 1989; Fleischer 2002; Politov 2017; Politov et al. 2000). Investigation of hybrid coregonines with genomic techniques is an area needing research in Beringia at both ancient and recent timeframes to characterize the outcomes of this process and its role in persistence and speciation of Beringian Coregoninae.

Epigenetic variation

Heritable variation may not necessarily be genetic, and heritable non-genetic variation—epigenetic variation—is gaining recognition in contributing to life-history variation and adaptation in fishes by acting on gene expression (e.g. Jeremias et al. 2018). Threespine Stickleback epigenetic studies have revealed differential methylation of ion channel encoding genes that have previously been identified to be under selection in freshwater populations (Artemov et al. 2017). Artemov et al. (2017) also observed immediate and sustained responses to the move to a freshwater environment in Threespine Sticklebacks, and hypothesize that the increased epigenetic plasticity in freshwater Threespine Sticklebacks may be compensatory to the lower genetic variation present compared to marine Threespine Sticklebacks. Life-history variation in

Rainbow Trout, between anadromous and resident ecotypes, has been shown to have epigenetic contributions affecting migration-related pathways, such as the circadian rhythm pathway (Baerwald et al. 2015). These examples and other work on climate-related adaptation in organisms (Jeremias et al. 2018), strongly suggests that the role of epigenetics should be explored in the context of Beringian fishes.

For primary freshwater fishes, the question of if epigenetic variation is compensatory for reduced genetic variation may be a key line of inquiry. For secondary freshwater fishes and anadromous and amphidromous fishes exhibiting a portfolio of life history diversity, the genetic vs epigenetic contributions to life history diversity is another key potential research theme in Beringia.

Defining units for conservation in Beringia

Freshwater fishes in Beringia may be characterized by very large distributions, e.g. Burbot, Northern Pike and the Arctic Charr complex. The entire biogeographic region of Beringia exhibits little endemism of species, perhaps one to three, within the genus *Dallia* (Balushkin and Chershnev 1982; Campbell et al. 2015; Campbell and Lopéz 2014; Chershnev and Balushkin 1981). The geographic range of *Dallia* dwarfs that of many other fish species found in southern latitudes and is only relatively small when compared to species or species complexes with Holarctic distributions. Certainly, research bias may be at work, and unrecognized species may exist. But, overall, the species diversity of Beringia may be considered low and fishes present generally have large distributions. A widespread geographic distribution like that typical of many Beringian fishes may mislead conservation efforts through several ways. Firstly, it may be thought that a widespread species is secure. Secondly, across large geographic ranges, there are diverse biotic or abiotic opportunities for local adaptation, such as alternative species interactions or geothermal springs that may generate locally adapted populations (e.g. Taylor et al. 2013). Thirdly, there may also exist unrecognized species diversity over large geographic scales that has not been identified, the Linnean Shortfall (Brown and Lomolino 1998). In the case of Beringian fishes, while there may be unrecognized species diversity, there is substantial within-species

diversity that should be recognized for conservation purposes.

Frameworks for recognizing intraspecific diversity include the United States Endangered Species Act, which recognizes Distinct Population Segments (DPSs). A DPS considers factors such as discreteness, significance, and status (U.S. Fish and Wildlife Service and National Oceanic and Atmospheric Administration 1996). As an alternative, the Evolutionarily Significant Unit (ESU) originated to help identify ‘distinct’ entities within species. For Pacific salmon (Waples 1991), two criteria were considered. Firstly, a population must be reproductively isolated from other conspecific units. Secondly, a population must represent an important component in the evolutionary legacy of the species. While the Evolutionarily Significant Unit is widely applied, for example to Pacific salmon in the contiguous United States, these frameworks are not widely applied to fish species that have not been identified as of conservation concern.

Nevertheless, frameworks such as DPSs or ESUs could be applied to help delimit intraspecific units in Beringian fishes. Along these lines, the identification of Designatable Units (DUs) has been applied to Beringian taxa, for example the Lake Whitefish species complex (Mee et al. 2015) and the East Beringian Lake Chub (Taylor et al. 2013; COSEWIC 2015). The DU framework permits identification and recognition of distinctive populations below the species level. What a species depends on the accepted taxonomic hierarchy for those organisms and the concept attempts to provide guidelines for recognition of DUs for conservation of biological diversity within whatever a species may be. As described previously within this manuscript, *Coregonus* species are not characterized well by Linnean taxonomy and have complex relationships with genealogical and phenotypic diversity. Within a single lake, there may be sympatric ‘species pairs’ or ‘trophic ecotypes’ that are reproductively isolated, such as the *Coregonus lavaretus* benthic and limnetic pairs of Dezadeash Lake (Bernatchez et al. 1996; Bodaly 1979). There are also phylogenetic divisions apparent within the Lake Whitefish Complex, and it is distributed across major phylogeographic regions. Within the Canadian distribution of the Lake Whitefish species complex, application of the DU framework led to the recognition of 36 DUs based on four criteria: (1) reproductive isolation, (2) phylogeographic groups, (3) local

adaptation, and, (4) biogeographic regions (Mee et al. 2015). Application of the DU framework to Lake Chub across its range in North America identified 12 DUs. Considering the phylogenetic diversity of Lake Chub, Eastern and Western ranges of this species have two mtDNA lineages that are 3.8% divergent. Combined with physiological phenotypes (associated with thermal or non-thermal springs) and biogeographic regions, a resulting 12 DUs were obtained.

A natural line of inquiry would be to apply this same framework to the entire Beringian distribution of the Lake Whitefish complex and other species or species complexes within Beringia. The resulting identification of practical units of conservation that exist below the species level and that are not recognized by the current taxonomic scheme will assist in ensuring the biological conservation of these fish species and complexes.

Conclusion

The broad taxonomic diversity and distributional range of Beringian fish combined with scientific studies to date leaves several open research directions that fit within the broader subject of Beringian fish phylogeography. Genetic and otolith microchemistry studies can inform basic, but unanswered biological questions of how much and if trans-Bering strait movements are ongoing or only historical; when and where numerous species and species complexes originated; and if a core refugium existed. A few lineages of Beringian fishes may represent distinct undescribed species. However, the definition of conservation units that accommodate below species definitions, as recently discussed, would benefit greatly from further efforts as we suggest. The examples of a poor fit of traditional taxonomy highlighted by some Beringian fishes further underscores how evolutionary concepts based on temperate or tropical organisms may poorly describe Beringian fishes. Research bias like this in flatfishes (Pleuronectiformes), where a high degree of effort in the low-diversity temperate regions of North American and Europe and much lower efforts in the tropical high diversity parts of the lineage’s range had effects on research into the higher taxonomy and evolutionary origins flatfishes (e.g. Campbell et al. 2019). The study of Beringian fish phylogeography, for example, may develop unique

interpretations of the role of genetic diversity, adaptive introgression and epigenetics in the survival of fishes in the dynamic environment of the North.

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Data availability The data analyzed during the current study were publicly available from GenBank from previous publications <https://www.ncbi.nlm.nih.gov/genbank/>. Alignment, treefiles and scripts to generate files are available at <https://github.com/MacCampbell/RFBF-beringian-fishes>.

Declarations

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